SEXUAL AND ONTOGENETIC DIMORPHISM IN OTOLITHS OF THE FAMILY OPHIDIIDAE

by

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ABSTRACT. - Sexual dimorphism in otoliths is recorded here for the first time (except for a single report in Cichlidae by Gaemers and Crapon de Crapona, 1986). Within the genus *Neobythites* about half of the species exhibit sexual dimorphism, whereas the other half does not. Morphological alteration only occurs in the otoliths of males and is always very much of the same nature. The change is so evident that male otoliths can easily be recognized as such. Otoliths of female fishes remain practically unchanged. Sexual dimorphism in otoliths is also evident from the monotypic genus *Spectrunculus*, a genus which is also known for its highly sexually dimorphic swimbladder pattern. The function and role of the observed sexual dimorphism in the social life of the fishes is not known. An obvious explanation would be a specific sound receiving ability designed to locate mating partners in the deepsea, where they live. A review of the few fossil otolith records related to both genera not only revealed three new species described here, but also brought to light several likely cases of sexual dimorphism in previously described species hitherto erected as separate species. One species is a *Neobythites* from the Australian Eocene and three other possible cases from the European Tertiary from the genus *Hoplobrotula*. This implicates, that sexual dimorphism of otoliths was already achieved at a relatively early stage in the history of these genera. An unusual case of ontogenetic dimorphism is observed in the genera *Spectrunculus* and *Pycnocraspedum*, in which otoliths of juvenile fishes in a way seem to be more 'specialized' than those of adults. This observation probably relates to the pelagic life style of the juveniles and the more benthic life style of adults.

RÉSUMÉ. - Un dimorphisme sexuel dans des otolithes est rapporté ici pour la première fois (à l'exception de celui qui a été décrit chez les Cichlidae par Gaemers et Crapon de Crapona, 1986). Dans le genre *Neobythites*, environ la moitié des espèces présente un dimorphisme sexuel, tandis que l'autre moitié n'en montre pas. L'altération morphologique des otolithes se produit uniquement chez les mâles et elle est très souvent de même nature. Ce changement est si évident que les otolithes des mâles peuvent aisément être repérés comme tels. Les otholithes des femelles demeurent pratiquement inchangés. Un dimorphisme sexuel des otolithes est aussi évident pour le genre monotypique *Spectrunculus* qui est aussi connu pour son fort dimorphisme sexuel de la vessie natatoire. La fonction et le rôle du dimorphisme sexuel des otolithes dans la vie sociale des poissons ne sont pas connus. Peut-être servent-ils à percevoir des sons pour localiser les partenaires de sexe opposé dans les profondeurs où ils vivent. Une revue des quelques données relatives à des otolithes fossiles rapportés à ces deux genres a permis de révéler non seulement l'existence de trois nouvelles espèces, qui sont décrites ici, mais aussi plusieurs cas probables de dimorphisme sexuel chez des espèces qui avaient été précédemment reconnues comme espèces à part entière. L'une d'elle est un *Neobythites* de l'Eocène australien et trois autres cas possibles pour le genre *Hoplobrotula* du Tertiaire européen. Cela implique que le dimorphisme sexuel était déjà présent dans les otolithes à un stade relativement précoce de l'histoire de ces genres. Un cas peu courant de dimorphisme ontogénétique a été observé chez les genres *Spectrunculus* et *Pycnocraspedum* chez lesquels les otolithes des juvéniles semblent plus "spécialisés" que ceux des adultes. Cette observation a probablement un rapport avec la vie pélagique des juvéniles alors que les adultes sont plus benthiques.

Key-words. - Ophidiidae, *Neobythites*, *Spectrunculus*, *Pycnocraspedum*, *Hoplobrotula*, Otoliths, Sexual dimorphism, Ontogenetic dimorphism, New fossil species.

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In 1990 I had the opportunity to extract otoliths from a large number of recent *Neobythites* species currently being investigated and reviewed by Jørgen Nielsen in Copenhagen. While extracting the otoliths it soon appeared that some of the species had otoliths with two quite distinct morphologies. On closer examination it was found that this phenomenon reflects sexual dimorphism.

This is the first clear case of sexual dimorphism recorded from otoliths (sexual dimorphism reported from otoliths of certain Cichlidae by Gaemers and Crapon de Crapona in 1986 to me is not very convincing). Scientists working taxonomically with otoliths, be it recent or fossil, should now be aware that such phenomenon can occur.

Sexual dimorphism is also found in the swimbladder of certain genera of the Ophidiidae (Howes, 1992), viz. genus *Spectrunculus*. Sexual dimorphism in the otoliths of this genus is also clearly evident (material was kindly made available by Nigel Merrett, London). Another genus with sexually dimorphic swimbladder patterns is *Glyptophidium* (pers. comm. Nielsen). In their otoliths, however, sexual dimorphism could not be observed. This implies, that swimbladder and otolith development may not be strictly interdependent.

OTOLITHS OF THE GENUS *NEOBYTHITES*

The otoliths of the genus *Neobythites* exhibit a rather typical ophidiid-type morphology, characterized by a shallow, straight sulcus with flat and well marked colliculi and a pseudoostial sulcus opening. The ostium including the ostial colliculi is about two times as long as the cauda. At the junction of the ostium and the cauda the upper margin of the sulcus is straight, whereas the lower margin shows a small but distinct indentation. Ostium and cauda are of about the same height. Generally, ostial and caudal colliculi are well separated, but there is a certain tendency within the genus to develop fused colliculi similar to so many other ophidiiform lineages (Schwarzhans, 1981). The sulcus itself is relatively long, nearly reaching as close to the posterior tip of the otolith as to the anterior. An ostial channel commonly connects the anterior tip of the ostium with the anterior tip of the otolith. In outline *Neobythites* otoliths are usually oval to elongate, about 1.5 to 2 times longer than high. Anterior and posterior tips usually occupy midaxial positions. The ventral rim is always gently curving, usually quite shallow, but the dorsal rim may exhibit a variety of pre- and postdorsal angles, sometimes with ornamentations.

The genero-typic morphology of *Neobythites* otoliths, as described above, is neither very plesiomorphic nor particularly derived in comparison to other Ophidiiformes. Typical plesiomorphic features as interpreted from assumed plesiomorphic members of the various ophidiiform families and subfamilies would for instance include a somewhat curving, slightly narrowed and deepened cauda more distinctly separated from the ostium along the ventral margin of the sulcus (Schwarzhans, 1981). On the other hand, the relative length of the sulcus, its pseudoostial opening, the clear separation of the colliculi and their proportions are thought to represent a rather plesiomorphic character status.

In general terms, recognition of *Neobythites* otoliths from the above diagnosis is not very difficult. However, in some instances distinction from otoliths of other, possibly related, genera can be quite subtle. Similar looking otolith morphologies are known from certain species of the genera *Monomitopus* (Fig. 93), *Hoplobrotula* (Fig. 106) or adult *Pycnocraspedum* (Fig. 96, 98) specimens. Otoliths of the genus *Benthocometes*, probably the most closely related living genus, are characterized by a much expanded dorsal area above the sulcus and an ostium which is less than 1.5 times the length of the cauda (Fig. 84). Otoliths of a new recent genus - to be described by Machida (unpubl. data) - and assumed to be closely related to *Neobythites* are characterized by completely fused colliculi and a sulcus which is much reduced in length (Fig. 85-86).

The recent species record

Species of the genus *Neobythites* are distributed circumtropically (except for the tropical East Atlantic) and inhabit bathyal depth. They seem to be particularly adapted to a benthopelagic life on the lower continental and island slopes.

The genus *Neobythites* is probably the most specious of all ophidioids. Cohen and Nielsen (1978) reported 14 nominally valid species within this genus, but noted that a thorough revision was much in need. Recently, Nielsen (unpubl. data) boosted the species count to a total of 40-45 including about 25 to be described as new. Through the kind help of J. Nielsen I have had the opportunity to study otoliths from all 17 described species and from 21 of the yet undescribed spp. The latter are named here in accordance to Nielsen's working codes - sp.1 to sp.28 (includes gaps from apparent synonymization).

As it seems now, the majority of the species - new or established ones - exhibit a remarkable provincialism as far as geographical distribution is concerned. For instance, *N. multistriatus* is entirely restricted to the waters around the Islands of Reunion and Mauritius. *N. analis*, *N.* sp.2 and *N.* sp.3, as another example, are only known from off Madagascar and the southeastern tip of Africa; *N. bimarginatus* from New Caledonia. The largest number of species is reported from the Indian and the West Pacific Oceans. In the East Pacific and the West Atlantic - along the shores of tropical America - the number of species is much smaller.

Sexual dimorphism in *Neobythites* otoliths

In total, otoliths of about 180 specimens of the genus *Neobythites* have been investigated representing 17 described and 21 undescribed species. From the majority of these the sex has been identified. 16 species definitely exhibit sexual dimorphism in their otoliths. Except for the otolith morphology, however, sexual dimorphism is not apparent in these fishes (though swimbladder patterns still remain to be investigated).

Apparently, sexual dimorphism in these otoliths affects only the morphology of male specimens, whereas female otolith morphology has remained virtually unchanged when being compared to species without sexual dimorphism. Also, the morphological alterations in male otoliths is always of the same style. Consequently, the presence of sexual dimorphism can even be interpreted in those cases, where only morphologically altered male specimens are known from a given species. This accounts for 5 species out of the 16 with observed sexual dimorphism. On the other hand, the genus *Neobythites* also includes at least 16 species without sexual dimorphism including species from which only morphologically unaltered male specimens are known to date. The status of the remaining 6 species, from which only female otoliths are known, must at present be regarded as unsolved.

The morphological differences observed in male otoliths can be described as follows and in descending order of importance.

1. Male otoliths are usually larger than female otoliths from fishes of about the same size.
2. Male otoliths are often much thicker than female otoliths.

3. In male otoliths the inner face is much more convex and smoother than in female otoliths.
4. Male otoliths exhibit a much more rounded dorsal rim than female otoliths.
5. Male otoliths are usually more compressed than female otoliths.
6. Quite often the separation of the colliculi is more pronounced in female than in male otoliths.
7. The proportions of the sulcus often differ in male and female otoliths.

In general terms it can be stated that:

1. Male otoliths can be readily recognized as such.
2. The morphological differentiation of species using male otoliths is often more subtle than that based on female otoliths.
3. Assigning isolated male and female otoliths to a certain species is only possible when both morphologies have previously been investigated by *'in situ'* material or maybe also in those rare instances where only a single species is known to occur in a given geographic frame.

This clear cut type of sexual dimorphism in ophidioid otoliths is so far a unique feature among teleosts. In the genus *Neobythites* it only occurs in a limited number of species. Furthermore, the kind of morphological alteration due to sexual dimorphism in male otoliths of *Neobythites* differs considerably from that observed in the genus *Spectrunculus* (see below). In my opinion it is therefore only fair to asssume that this feature was achieved only once in the evolutionary history of the genus and thus represents a true synapomorph character combining the respective species in a single defined phylogenetic lineage.

Table I lists all recent species of the genus *Neobythites* of which otoliths have been investigated and their respective status as far as sexual dimorphism is concerned.

Within the large group of species with sexually dimorphic otoliths, there are some of seemingly closer relationships clustering in species groups.

One group for instance comprises the species *N. analis*, *N. macrops*, *N. fasciatus*, *N. multistriatus*, *N.* sp.2 and *N.* sp.3. They are all characterized by relatively elongate otoliths, both male and female. But the thickness is extremely diachronous in both sexes: male otoliths are much thicker than female otoliths. The dorsal rim of male otoliths is somewhat irregular, not completely smoothed. Typically, the sulcus is wider in males than in females, except for *N. analis*.

A second group comprises the species *N.* sp.14, *N.* sp.19 and possibly *N.* sp.16. They differ from the previous group in three aspects of the male otolith morphology: the dorsal rim is almost perfectly smoothed and rounded, the sulcus is not wider than in females and the outer face of male otoliths is flat to slightly concave resulting in a more fragile appearance of the otolith. According to female morphology *N.* sp.14 can be divided into two separate morphotypes, termed here *N.* sp.14 and *N.* sp.14a, which also seem to be geographically separated.

A third group comprises relatively compressed otoliths otherwise resembling morphologically those of group two. The species placed here are *N. bimarginatus*, *N.* sp.17, *N.* sp.23 and *N.* sp.15. The latter two species are morphologically intermediate between group two and three.

The four American species seem to be clearly separated from the above Indo-West-Pacific ones. Furthermore, they comprise two rather distinct morphologies. One is represented by *N. marginatus* (and possibly the related *N.* sp.1). Here, the male otoliths are

Table I. - All recent species of the genus *Neobythites* of which otoliths have been investigated and their respective status as far as sexual dimorphism is concerned.

Species with sexually dimorphic otoliths. Males and females investigated		
Neobythites analis	Figs 1-2	11 spec.
Neobythites fasciatus	Figs 4-5	3 spec.
Neobythites gilli	Figs 38-39	6 spec.
Neobythites macrops	Fig. 3	6 spec.
Neobythites marginatus	Figs 32-35	17 spec.
Neobythites multistriatus	Figs 23-24	4 spec.
Neobythites sp.2	Figs 6-11	13 spec.
Neobythites sp.3	Figs 12-14	4 spec.
Neobythites sp.14 and sp.14a	Figs 15-20	8 spec.
Neobythites sp.15	Figs 27-28	4 spec.
Neobythites sp.23	Figs 25-26	2 spec.
Species with inferred sexually dimorphic otoliths. Only males investigated		
Neobythites bimarginatus	Fig. 29	1 spec.
Neobythites ocellatus	Fig. 37	1 spec.
Neobythites sp.12 (assumed male)	Fig. 40	1 spec.
Neobythites sp.17	Figs 30-31	2 spec.
Neobythites sp.19	Fig. 21	1 spec.
Species without sexually dimorphic otoliths. Males and females investigated		
Neobythites longipes	Figs 52-54	7 spec.
Neobythites malayanus	Figs 46-47	7 spec.
Neobythites nigromaculatus	Figs 55-56	6 spec.
Neobythites purus	Figs 65-66	3 spec.
Neobythites sivicola (assumed)	Figs 59-60	6 spec.
Neobythites trifilis	Figs 48-50	11 spec.
Neobythites sp.5	Figs 73-75	7 spec.
Neobythites sp.10	Figs 43-45	9 spec.
Neobythites sp.11	Figs 61-64	9 spec.
Neobythites sp.24	Figs 76-77	3 spec.
Neobythites sp.28	Fig. 67	3 spec.
Species assumably without sexually dimorphic otoliths. Only males investigated		
Neobythites steatiticus (assumed)	Fig. 41	1 spec.
Neobythites stelliferoides (assumed)	Fig. 42	3 spec.
Neobythites sp.7	Fig. 70	1 spec.
Neobythites sp.13 (male?)	Fig. 51	1 spec.
Neobythites sp.18	Fig. 68	2 spec.
Status of sexual dimorphism unknown. Only females investigated		
Neobythites stigmosus	Fig. 69	3 spec.
Neobythites sp.1 (sex not identified) (?close to *N. marginatus*)	Fig. 36	3 spec.
Neobythites sp.6	Fig. 71	1 spec.
Neobythites sp.16 (?close to *N.* sp.14)	Fig. 22	1 spec.
Neobythites sp.22	Figs 57-58	3 spec.
Neobythites sp.26	Fig. 72	2 spec.

very compact and massive, but the dorsal rim is still somewhat angular. Both females and males are quite elongate and in fact differ less from each other than in most other species. In contrast, otoliths of *N. gilli* and *N. ocellatus* are amongst the most compressed in the genus *Neobythites*. However, all four American species have one character in common: the sulcus in male otoliths is thinner than in females.

The species without sexual dimorphism can also be grouped into morphologically separated entities according to their otolith morphology. Some of the species, however, exhibit some kind of 'incipient' sexual dimorphism. For instance in *N. nigromaculatus* the inner face of male otoliths is slightly more convex than that of females and in *N.* sp.24 the male otolith seems slightly more roundish and compressed. These subtle differences will probably submerge in the 'general intraspecific variability', once more material is known. And even if it should prove statistically stable, such a minute difference would not qualify the species in question to be placed in the group with true sexual dimorphism as described before.

A group readily distinguishable from the rest comprises the species *N. malayanus, N. steatiticus, N. stelliferoides* and *N.* sp.10. They all have rather compressed otoliths with a blunt posterior tip and an unusually flat inner face. The sulcus is rather wide and the colliculi are well separated.

A second, equally well defined group includes otoliths with an elongate to very elongate shape and a pointed, somewhat downwardly moved posterior tip. In this group I place *N. longipes, N. nigromaculatus, N. purus, N. sivicola, N.* sp.11, *N.* sp.13, *N.* sp.22 and *N.* sp.28. *N. longipes* differs from the others in exhibiting the most elongate otolith shape and a relatively long cauda. *N. sivicola* and *N.* sp.11 are unique for their ventrally somewhat widened cauda.

Of the remaining species *N. stigmosus, N.* sp.5, *N.* sp.6, *N.* sp.7, *N.* sp.24 and *N.* sp.26 all exhibit rather compressed otoliths. Other features, however, show certain pecularities that may not support a grouping of these species.

The fossil record of *Neobythites* otoliths

Ophidiiform otoliths are very common in the fossil record (unlike other fossil remains of ophidiiforms; a paradox not yet sufficiently explained, see Schwarzhans, 1993). They are particularly common in sediments of the warm shallow seas in the Early Tertiary and are known since the Upper Cretaceous. Some 20 years ago, when the knowledge of recent ophidiiform otoliths was still rather limited, several fossil otolith species were placed in the genus *Neobythites*. With growing knowledge (Nolf, 1980; Schwarzhans, 1981) it became apparent that most of these species represent fossil genera adapted to shallow warm seas. In fact, it is now evident that the order Ophidiiformes was much more specious and widespread in the Early Tertiary than it is today. Schwarzhans (1986) noted that of all the described fossil otolith-based species only three remain valid records of the genus *Neobythites*, and of these two must now be synonymized. In addition, two new fossil species of *Neobythites* are described. Amazingly, none of the fossil records originate from within the recent area of distribution of the genus. However, the marine sediments from the Indo-West-Pacific and Central America, where *Neobythites* now lives, have remained virtually unprospected for fossil otoliths. Therefore, I expect a much larger wealth of fossil *Neobythites* species to be discovered once fossil otoliths from there should become known.

Genus aff. *Neobythites laevis* Stinton, 1977

syn. 1977 - *Neobythites laevis* Stinton - Pl. 8, Fig. 5.

Remarks. - This species from the Middle Eocene of the Hampshire Basin, southern England, is the earliest possible record of the genus. The unique type specimen is refigured on figure 78. Its placement in the genus *Neobythites* at present remains somewhat provisional and needs further verification by additional material.

Neobythites verus Schwarzhans, 1986

syn. 1986 - *Neobythites verus* Schwarzhans - Fig. 67 - **female**.

syn. 1986 - *Neobythites inprobus* Schwarzhans - Figs. 68-71 - **male**.

Remarks. - These two nominal species had been described from the Upper Eocene of the St. Vincent and Murray Basins in South Australia. In my original description I was surprised that two *Neobythites* species would occur simultaneously (Schwarzhans, 1986, p. 37). As it turns out now, after sexual dimorphism has become known from recent species of the genus, the two nominal species very likely represent male and female morphologies from a single species. It would then appear that *N. verus* represents the female morphology and *N. inprobus* the male morphology.

With all likelihood, *N. verus* must now be regarded as the earliest fossil record of sexual dimorphism in that genus. This also implies that the achievement of this phenomenon dates unexpectedly far back into geological time and that the various 'species groups' tentatively proposed for the genus *Neobythites* have been phylogenetically separated from each other for an extended period of time.

The holotype of *N. verus* is refigured in figure 79 and that of *N. inprobus* in figure 80.

Neobythites joenielseni n. sp.

syn. 1980 - *Neobythites* sp. Schwarzhans - Fig. 399.

Holotype. - BSP (leg. Pfeil), Fig. 81. Type location: GS 9685, Pukeuri road cut, Otago, New Zealand South Island. Type stratum: Altonian, Lower Miocene.

Paratype. - GSNZ, Fig. 82. GS 3341, Karoro brick work, Westland, New Zealand South Island. Waiauan, Middle Miocene.

Etymology. - Named after Jørgen Nielsen, Copenhagen, who made this large collection of recent *Neobythites* otoliths available to me.

Diagnosis. - Elongate, flat, thin otoliths, about two times as long as high. Ostial colliculum 2.3 times as long as caudal colliculum. Dorsal rim with prominent predosal angle and backwardly shifted postdorsal angle. Mediodorsal portion straight. Posterior tip of otolith pointed.

Description. - Otoliths of this species are rather elongate, two times as long as high and thin. Anterior and posterior tips of the otolith are pointed along the axis of the sulcus. The dorsal rim shows a prominent predorsal angle and a far backwardly shifted postdorsal angle. Pre-, medio- and postdorsal portions of the rim are all straight, the pre- and postdorsal portions inclined, the mediodorsal portion nearly horizontal. The ventral rim is shallow, gently curving, deepest anteriorly.

The inner face is flat, smooth, with a long sulcus in a slightly inframedian position. The ostium is about 2.3 times as long as the cauda. Ostial and caudal colliculi are well separated. The dorsal depression is relatively large, but flat.

The outer face is just slightly more convex than the inner face and virtually smooth.

Discussion. - *N. joenielseni* is the first record from New Zealand. The specimen previously recorded as *Neobythites* sp. by Schwarzhans (1980) was originally regarded as closely related to a recent specimen collected from off West Australia, which was then incorrectly identified as *N. gilli* (Schwarzhans, 1980, fig. 400), now placed in *N.* sp.22. The correlation itself, however, still remains valid. *N. joenielseni* is interpreted as a fossil species related to *Neobythites* species without sexual dimorphism grouped with such recent species as *N. purus* and *N.* sp.22.

Neobythites errabundus n.sp.

Holotype. - GPIM-M (leg. Wienrich), Fig. 83. - Type location: water well Laerhof, Kevelaer-Wetten, Northwest Germany. - Type stratum: Bislich sand, Reinbek, Middle Miocene.

Etymology. - *errabundus* (lat.) = roving, wandering; refering to the unusual geographic occurrence of the species.

Diagnosis. - Elongate, flat, thin otolith, about two times as long as high. Dorsal rim with prominent predorsal angle, but medio- and postdorsal portions poorly defined, both inclined and slightly ornamented. Sulcus slightly bent. Ostium more than three times as long as cauda.

Description. - The unique, very large and well preserved otolith of this species is rather elongate, two times as long as high and thin. Anterior and posterior tips of the otolith are pointed, situated slightly below the axis of the sulcus. The anterior portion of the dorsal rim up to the predorsal angle is straight, smooth and steeply inclined. The postdorsal angle is very weakly developed, shifted considerably towards anterior. Medio- and postdorsal portions are gently inclined and somewhat ornamented. The ventral rim is shallow and very gently curving.

The inner face is slightly convex along the horizontal axis, but virtually flat along the vertical axis. The sulcus is long, relatively wide, with a median position. The ostium is more than three times as long as the cauda. Ostial and caudal colliculi are relatively well separated. The dorsal depression is very faint; some radial furrows intrude onto the dorsal field from the marginal ornamentation. The ventral field shows an incipient ventral groove close to the ventral rim.

The outer face is flatter than the inner face and smooth, except for few radial furrows along the dorsal rim.

Discussion. - Although the Neogene sediments of the North Sea Basin have been intensively studied in the past for otoliths this is the first record of a *Neobythites* species from this region. In fact, its occurrence there is quite unexpected (hence the etymology).

Neobythites errabundus best resembles recent otoliths of the *N. purus* - *N. sivicola* group without sexual dimorphism in otolith morphology. It is readily recognized, however, by its very high ostial length to caudal length index (more than 3), which puts it somewhat apart from all the recent species.

OTOLITHS OF THE GENUS *SPECTRUNCULUS*

Like the otoliths of the genus *Neobythites*, those of the genus *Spectrunculus* also exhibit a rather typical ophidiid-type morphology. The sulcus is shallow, straight, positioned slightly inframedian with flat, well marked and separated colliculi. The ostium is about three times as long as the cauda and also somewhat wider. Anteriorly it does not open to the margin of the otolith, but is connected to it by a faint ostial channel. At the junction of the ostium with the cauda the upper margin of the sulcus is straight, whereas the lower margin shows a broad, distinct, somewhat s-shaped indentation. The ratio otolith length to sulcus length is 1.5 to 1.6. In outline *Spectrunculus* otoliths are oval to elongate, about 1.5 to 2 times longer than high. Anterior and posterior tips are usually pointed and occupy mid-axial positions. The ventral rim is always gently curving, but the dorsal rim usually exhibits an angular predorsal corner and a flat, nearly horizontal, long mediodorsal portion.

Spectrunculus otoliths exhibit a combination of plesiomorphic and apomorphic characters. Plesiomorphic features are the shape of the junction between ostium and cauda and the clear separation of the colliculi. More apomorphic characters are the reduced sulcus opening and the rather small cauda.

Otoliths of the genus *Spectrunculus* are not always easy to distinguish from those of other neobythitine genera with 'mildly' plesiomorphic otolith morphologies. Similar otoliths for instance are those of the genus *Hoplobrotula* (Fig. 106), although always with a pseudoostial sulcus opening and a much smaller ratio otolith length to sulcus length (see next chapter for further discussion). *Barathrodemus* (Fig. 92) and *Barathrites*, regarded by Cohen and Nielsen (1978) as probably related genera, exhibit otoliths with a strongly reduced sulcus morphology and completely fused colliculi. *Bassogigas* could also be a possible candidate for a closer relationship (Fig. 94-95). Its otoliths, although more elongate and somewhat different in shape, exhibit a similar sulcus organization. However, here the cauda and the caudal colliculum are even more strongly reduced in size and the indentation of the ventral sulcus margin at the ostial-caudal joint has disappeared. Finally, similar looking otoliths are known from certain species within the genus *Monomitopus* which is known to contain two quite different otolith morphologies. One group, comprising the two species *M. magnum* Carter & Cohen, 1985 (Fig. 93) and *M. nigripinnis* (Alcock, 1889) (the type-species), resembles both *Bassogigas* and *Neobythites* otoliths.

In their revision of the two nominal ophidiid genera *Spectrunculus* and *Parabassogigas* Nielsen and Hureau (1980) concluded that *Spectrunculus* Jordan & Thompson, 1914 (type species: *S. radcliffei* Jordan & Thompson, 1914) represents the postlarval stage and *Parabassogigas* Nybelin, 1957 (type species: *Sirembo grandis* Günther, 1877) the juvenile/adult stages of the same genus. Furthermore, the three nominal species of the former *Parabassogigas* and the one from *Spectrunculus* are regarded as a single species - *Spectrunculus grandis*.

The single recent species of the genus *Spectrunculus* is widely distributed in the Atlantic, Indian and Pacific Oceans. Juveniles and adults live on or near the bottom at 800-4255 m depth (main distribution between 2000 and 3000 m). Most catches are from the subtropical to temparate latitudes, commonly in association with upwelling systems (off northern SW-America, off California, off SW-Africa), but not always so (NW-Atlantic, off SW-Ireland) (Nielsen and Hureau, 1980). The postlarval stage occurs pelagically and is in some ways particularly adapted to this way of live.

Ontogenetic dimorphism in *Spectrunculus* and *Pycnocraspedum* otoliths

Otoliths of the pelagic postlarval stage of *Spectrunculus* are unknown, but those of juveniles and adults have been studied and exhibit a remarkably high degree of ontogenetic differentiation (Schwarzhans, 1981). In *Pycnocraspedum* too, juveniles are adapted to a pelagic way of life whereas adults live benthically at moderate depth. This genus shows the most dramatic ontogenetic differentiation so far observed in teleost otoliths. In fact, when only a juvenile otolith was known of *Pycnocraspedum* in 1981, I placed a large fossil otolith (*P. cetonaensis*) in a then newly erected fossil genus *Paragenypterus* Schwarzhans, 1981 (Figs 96-98). Only now that large, recent *Pycnocraspedum* otoliths have become available have the extreme ontogentic morphological changes been realized and *Paragenypterus* must now be regarded as a junior synonym of *Pycnocraspedum* (the fossil species, however, with its clearly separated colliculi remains valid; Fig. 98).

In both genera (although to different degrees) juvenile otoliths are more compressed and in the case of *Pycnocraspedum* even exhibit a completely different outline. Also in both genera, particularly in *Pycnocraspedum*, juveniles show a much shorter sulcus than adults if compared to the relative length of the respective otoliths. In a way, the whole sulcus morphology of the juveniles seems to be reduced. For instance in *Spectrunculus* the ventral indentation at the junction of ostium and cauda is much weaker in juveniles than in adults and also the reduction of the size of the cauda is much less developed. These reductions of the sulcus morphology is a widespread development in many other ophidiiform lineages, but there they principally characterize the more advanced members of it.

It seems that the ontogenetic differences as described above from the two genera in question can not be explained by simple allometric ontogenetic growth, whereby juvenile otoliths exhibit a somewhat more 'generalized' morphology as compared to adults. In my opinion the juvenile otoliths of the two genera exhibit some degree of specialization of their own. This may to a certain degree reflect the adaption of the postlarval / early juvenile fishes to their pelagic way of living.

I therefore propose to call these kinds of ontogenetic changes 'ontogenetic dimorphism'.

Sexual dimorphism in *Spectrunculus* otoliths

In contrast to fishes of the genus *Neobythites* where sexual recognition of the specimens often requires microscopic investigation of the gonads, in the genus *Spectrunculus* the fishes themselves exhibit a certain degree of sexual dimorphism. Nielsen and Hureau (1980) reported that freshly caught males are dusky cream in colour and females light brown. The number of dorsal and anal fin-rays and the total number of vertebrae is higher in males than in females. Finally, G. Howes (London, pers. comm.) pointed out that certain neobythitine fishes exhibit a sexually dimorphic swimbladder pattern with that of males being the most specialized one. In his words the swimbladders of the genus *Spectrunculus* are clearly the ones with the highest degree of sexual dimorphism.

This was the reason why *Spectrunculus* was selected as a second case to test the development of sexual dimorphism of otolith morphology. Otoliths from about a dozen *Spectrunculus* specimens kindly made available by N. Merrett (BMNH, London) indeed also revealed a certain degree of sexual dimorphism. Again it seems to be the males that exhibit the altered morphology. However, the type of alteration is different from that observed in the genus *Neobythites* and the degree of sexual dimorphism is also much smaller. This in my opinion shows that although some kind of interaction between swimbladder and otolith development is quite likely and would logically be expected it can not be a straight counteractive one. This fact also suggests that sexual dimorphism in *Neobythites* and *Spectrunculus* had developed independently.

The structure of morphologic alterations observed in male otoliths can be described as follows and in descending order of importance.

1. Male otoliths are more compressed than female otoliths.
2. The posterior tip of the otolith is blunt and massive in males, pointed in females.

3. The anterior tip of the otolith is more rounded and shifted dorsally in males, angular and with a midaxial position in females.
4. The predorsal angle is reduced in males.
5. Male otoliths exhibit a much deeper curving ventral rim than female otoliths.
6. In comparison to the length of the otolith the sulcus is relatively longer in male otoliths than in female otoliths.

Comparing the morphological alterations of males of the genus *Spectrunculus* with that of males from *Neobythites* it can be concluded that:

1. In *Spectrunculus* mainly characters of the outline of the otolith are affected.
2. In *Neobythites* the size of the otolith, characters of the outline, curvature of the inner and outer faces and characters of the sulcus morphology are affected in about equal amounts.

POSSIBLE SEXUAL DIMORPHISM IN FOSSIL SPECIES OF THE GENUS *HOPLOBROTULA*

There is a certain group of neobythitine otoliths in the Oligo-/Miocene of the North Sea Basin and the Mio-/Pliocene of the Mediterranean that regularly occurs in "pairs of species". One "species" is elongate and thinset, whereas its co-occuring counterpart is massive and compact. Traditionally, these "species" have been placed in the genus *Hoplobrotula*, but Schwarzhans (1981) has also proposed to place the compact forms into the genus *Spectrunculus*. Both are possible alternatives, but due to the pseudoostial opening of the sulcus *Hoplobrotula* at this stage seems to be the more appropriate generic assignment.

In the present light of sexual dimorphism it is very tempting to regard these "species pairs" as male and female morphologies of a single species. And this is in fact my recommendation. Based on this hypothesis the style of morphologic alterations in the assumed male otoliths can be described as follows.

1. Male otoliths are much more compressed and thickset than female otoliths.
2. The posterior tip of the otolith is pointed in female otoliths, blunt or rounded in males.
3. Male otoliths show a broadly rounded predorsal rim, female otoliths a distinct, sometimes protruding predorsal angle.

Compared to recent otoliths of the genus *Hoplobrotula* (Fig. 106) the supposed female morphology would fit perfectly into the generic assignment. However, the three recent *Hoplobrotula* species, which are restricted geographically to the realms of the Indo-West-Pacific, seemingly do not exhibit any sexual dimorphism in otolith morphology or very faintly so. The supposed male morphology of the fossil species somewhat resemble members of the genus *Spectrunculus*, a genus with well established sexual dimorphism. In any instance, the fossil species from the European Tertiary should not directly be alligned phylogenetically with any of the recent species, be it from the genus *Hoplobrotula* or *Spectrunculus*. Most certainly they represent an extinct fossil lineage. With that in mind and the observation that another genus (*Neobythites*) contains both lineages with and without sexually dimorphic otoliths I provisionally leave the following fossil species with the genus *Hoplobrotula*.

Hoplobrotula difformis (Koken, 1884)

syn. 1884 - Ot. (*Gadidarum*) *difformis* Koken - Pl. 11, Fig. 11 (vide Koken, 1891) - **male**

syn. 1884 - Ot. *(Gadidarum) acutangulus* Koken - Pl. 11, Fig. 13 (Koken, 1891) - **female**.

syn. 1891 - Ot. *(Ophidiidarum) difformis joachimicus* Koken - Pl. 1, Fig. 7 - **male**.

? syn. 1891 - Ot. *(Ophidiidarum) difformis hermsdorfensis* Koken - Pl. 6, Fig. 5 - **female**.

? syn. 1942 - Ot. *(Ophidiidarum) hilgendorfi elongata* Weiler - Pl. 14, Fig. 2 - **female**.

Remarks. - *H. difformis* and *H. acutangula* up to now have been regarded as two separate species in the literature. They are widely distributed and occur strictly parallel in sediments of the Middle Oligocene to Middle Miocene age in the North Sea Basin. Having investigated sexual dimorphism in recent otoliths of the genera *Neobythites* and *Spectrunculus* and the degree of morphological alteration, I now postulate that *H. difformis* represents the male morphology and *H. acutangula* the female morphology of the same species.

The slightly more elongate and larger supposed female forms of Miocene age have previously been regarded as another separate species - *H. elongata.* The supposed male morphologies may differ slightly from the older ones in being more rounded. But this difference is too faint to seem meaningful. However, as experienced in the genus *Neobythites*, specific differentiation based on female morphologies often seems to be easier than with male morphologies. At this stage it cannot be strictly ruled out that actually we are dealing with two stratigraphically separated but very closely related species.

A typical supposed male specimen from the Miocene is figured in figure 99, the lectotype of *H. joachimica* from the Middle Oligocene in figure 100 and the holotype of *H. elongata* in figure 101.

Hoplobrotula gibba (Bassoli, 1906)

syn. 1906 - Ot. *(Ophidium) gibbus* Bassoli - Pl. 1, Fig. 39-40 - **male**.

syn. 1970 - *Bauzaia tuberosa* Robba - Pl. 16, Fig. 1-2 - **female**.

syn. 1970 - *Bauzaia ornatissima* Robba - Pl. 16, Fig. 3-5 - **male**.

Remarks. - Like in the species before, *H. gibba* is regarded as the male morphology and *H. tuberosa* as the female morphology of the same species, although in this case the morphological differentiation of the sexes would be more drastic. Conspicuous again is the fact that the two morphologies occur strictly parallel in the Upper Miocene of Italy.

The nominal species *H. gibba* and *H. ornatissima* simply reflect different sizes of otoliths. *H. gibba,* the larger one, exhibits some kind of an anterior sulcus opening similar to the supposed female morphology of *H. tuberosa.* Again, when comparing the supposed male and female morphologies of *H. difformis* and *H. gibba,* specific differentiation is much easier with females than with males.

The holotype of *H. tuberosa* is redrawn from Robba, 1970 (Fig. 103). A supposed male morphology of *H. gibba* (though of a moderately sized specimen with a not yet anteriorly opened ostium) is shown in figure 102.

Hoplobrotula orcianensis n.sp.

Holotype. - BMNH P.41581, fig. 104. Type location: Orciano near Pisa, Toscana, northern Italy. Type stratum: Zanclian, Lower Pliocene.

Paratype. - BMNH P.41538, fig. 105. Topo- and strati-typic.

Etymology. - Named after the type location.

Diagnosis (supposed female morphology). - Elongate, moderately thickset otolith, about two times as long as high. Anterior tip rounded, posterior tip pointed. Dorsal rim with rounded predorsal portion. Sulcus wide.

Description. - Of the two investigated otoliths one is perfectly preserved, the other a bit eroded. Both represent supposed female morphologies. The otolith is moderately thickset, elongate, about two times as long as high, rounded anteriorly and distinctly pointed posteriorly. Both tips are situated at about midaxial position. The dorsal rim is gently curving, almost symmetrically to the ventral rim. Even the predorsal portion is gently rounded, the postdorsal portion somewhat irregularly undulating.

The inner face is moderately convex in vertical and horizontal directions and bears a very wide, midaxially positioned sulcus. The sulcus in fact is much wider than the colliculi, so that these look like being surrounded by a groove. The colliculi are flat, well marked and well separated. The ostial colliculum is about 2.5 times longer than the caudal colliculum and also wider. The junction of cauda and ostium at the ventral rim of the sulcus is only faintly marked. The ostial opening is truly pseudoostial, but with the ostial colliculum terminating at some distance from the anterior rim of the otolith.

The outer face is less convex than the inner face and very slightly and irregularly ornamented.

Discussion. - *H. orcianensis* most likely is the last true representative of the extinct lineage comprising also *H. difformis* and *H. gibba.* It is readily distinguished from the supposed female morphologies of these species by the gently curving dorsal rim, the more thickset appearance and proportions of the sulcus. No 'males' are known as yet.

DISCUSSION AND INTERPRETATION

Sexual dimorphism is rather common in teleosts fishes. Indubitable sexual dimorphism in the otolith morphology, however, is now being recorded for the first time, despite the many recent specimens investigated of many different teleost taxa. The observation refers to the ophidiid genera *Neobythites* and *Spectrunculus*. At least one of the two (*Spectrunculus*) is also known for its sexually dimorphic swimbladder pattern; this remains to be investigated in *Neobythites*. According to G. Howes (London, pers. comm.) there are more neobythitine genera with sexually dimorphic swimbladder patterns, and there may be more neobythitine genera with sexually dimorphic otolith morphologies, too. Furthermore, paleontologists dealing with fossil neobythitine otoliths should be aware of the eventuality of sexual dimorphism occuring. Some fossil examples refering to the genera *Neobythites* and *Hoplobrotula* have been discussed here and more are likely to surface in the future. Finally, once having been alerted to the occurrence of sexual dimorphism in otoliths , we may still expect further occurrence of this phenomenon in other teleost families.

Passing quickly through our present knowledge of the otoliths of the about 45 valid neobythitine genera (Nolf, 1980; Schwarzhans, 1981) I cannot with any certainty point to additional candidates for sexual dimorphism. Otoliths are known from most of these genera, but since many of them are very rare fishes the records are often singular. Also the sex of the fishes from which the otoliths have been obtained has rarely been identified. However, there are certain genera from which a considerable number of otolith specimens have been examined. They are: *Glyptophidium, Bassogigas, Hoplobrotula, Holcomyctero-*

nus, Dicrolene, Homostolus, Monomitopus (part) and *Bassozetus*. None of them exhibit any indication of sexual dimorphism in the otoliths (in respect to *Hoplobrotula* only true for recent species; see above). After all, sexual dimorphism in otoliths seems to remain a very rare phenomenon even in the Neobythitinae. But it obviously has developed independently in at least 2 recent lineages (plus one possible fossil).

What actually has caused this unique development of sexually dimorphic otoliths in the case of *Neobythites, Spectrunculus* or the fossil *Hoplobrotula* remains unknown for the time being. Too little is known about the functional morphology of otoliths and their interaction with other organs such as the swimbladder. In any case, otoliths are known to play an important role in the sound receiving ability of fishes. It could be speculated that the observed morphological alterations in male otoliths are designed to either receive specific (sound) signals from the females or produce such sounds. Such a mechanism could be helpfull for instance in the search of the right mating partner in the aphotic zone in which these fishes live. However, the two recent genera from which sexual dimorphism in otoliths has now been recorded differ fundamentally from each other in their evolutionary speciation and geographical distribution patterns. *Neobythites* probably is the genus with the largest number of species in the whole family. The high degree of speciation, unusual for deepsea fishes, seems to be a result of the restricted geographical distribution pattern of most species. In contrast the genus *Spectrunculus* contains a single species which is distributed almost cosmopolitically throughout the world oceans. Probably, the functional specialization of the otoliths that has resulted in sexual dimorphism has worked in different ways. In this respect it is of interest that the specialization of the postlarval stages of *Spectrunculus* and *Pycnocraspedum* to a pelagic way of living seemingly has also left its imprints on the otolith morphology of juveniles, which I have termed ontogenetic dimorphism.

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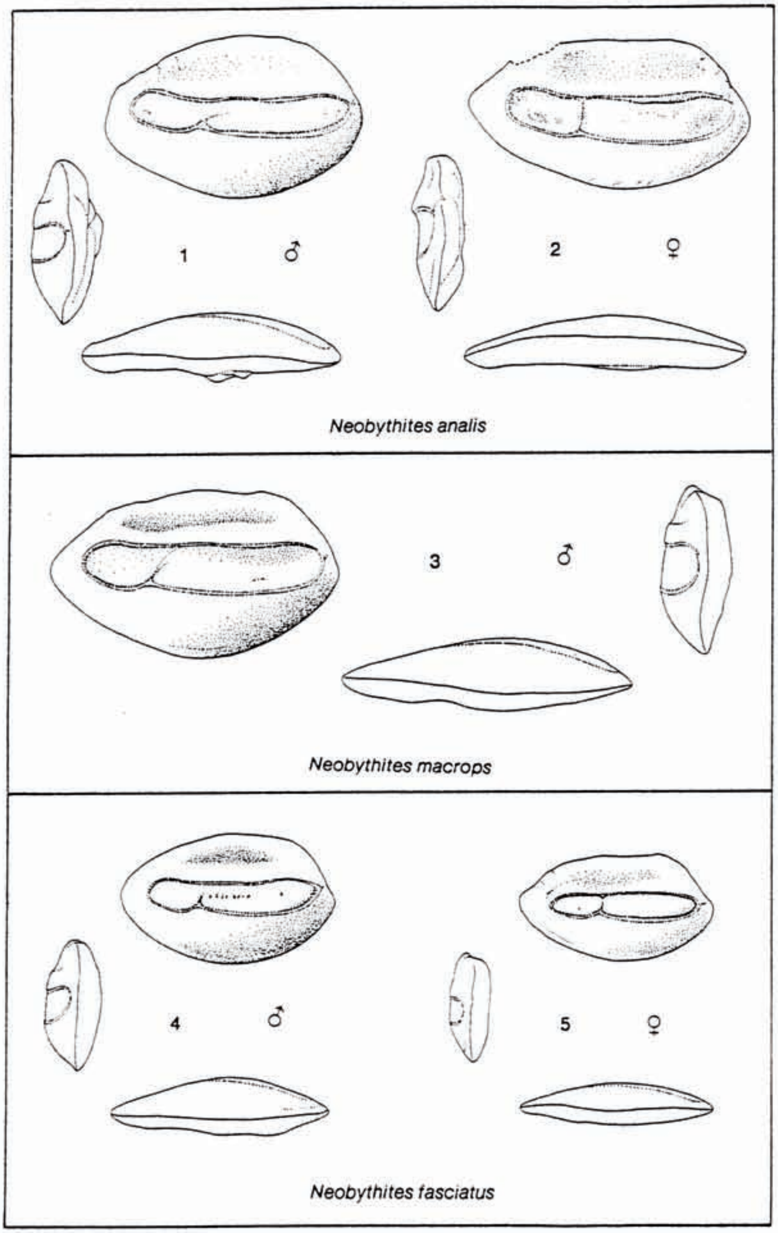
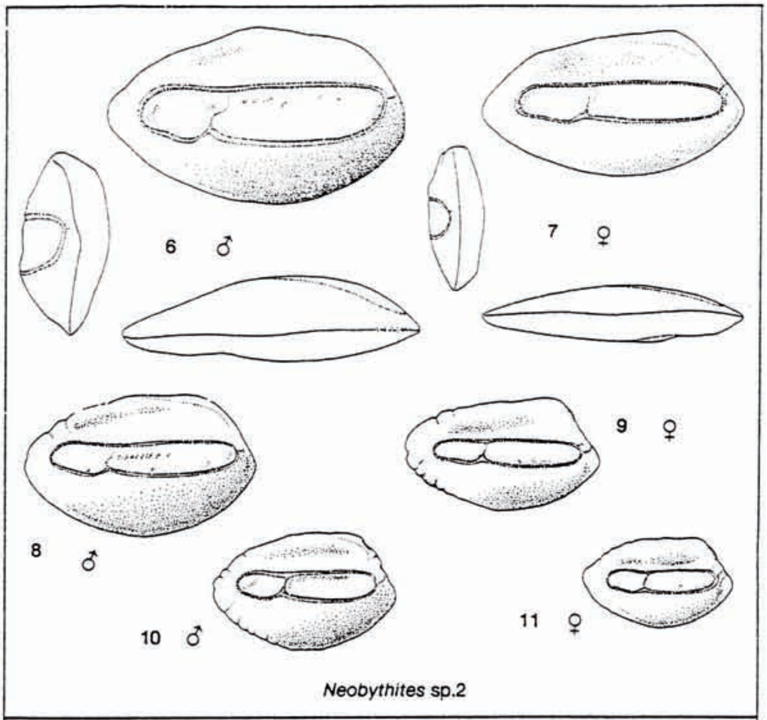
Explanation to figures

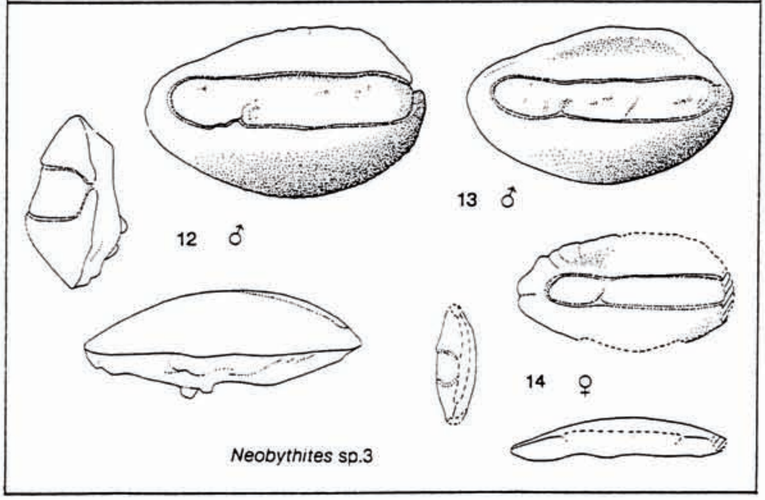
All recent otoliths shown are from the left side; the following figures show fossil otoliths from the right side - 78, 79, 80, 81, 83, 100, 105. Lateral views are from ventral except for figures 67, 79, 83, 85 and 96, which are views from dorsal, and views from anterior. Sexes are marked with symbols wherever known. Catalogue-numbers of recent otoliths refer to fishes from which the otoliths were taken. Three figure numbers following the prefix No. refer to preliminary working numbers of J. Nielsen. Whenever otoliths are catalogued separately, it is noted as such. Catalogue-numbers of fossil otoliths refer only to otoliths. The following catalogue-abbreviations are used.

AMS - Australian Museum, Sydney; BMNH - British Museum (Natural History), London; BSKU - Kochi University, Department of Biology, Kochi; BSP - Bayrische Staatssammlung Paläontologie, München; CSIRO - Commonwealth Scientific and Industrial Research Organization, Cronulla, New South Wales; GPIM - Geologisch-/Paläontologisches Institut der Universität Mainz; GSNZ - Geological Survey of New Zealand, Lower Hutt; IOAN - P.P. Shirov Institute of Oceanology, Moscow; IRSNB - Institut Royal des Sciences Naturelles de Belgique, Brussels; ISH - Institut für Seefischerei, Hamburg; JM - Japanese Museum, Tokyo; LACM - Los Angeles County Museum of Natural History, Los Angeles; MCZCM - Harvard University, Museum of Comparative Zoology, Cambridge,Massachusetts; MNHN - Muséum National d'Histoire Naturelle, Paris; RUSI - JLB Smith Institute of Ichthyology, Grahamstown; SADME - South Australian Department of Mines and Energy, Adelaide; SMF - Senckenberg Museum, Frankfurt; SOSC - Smithonian Institution Oceanographic Sorting Center; SU - Stanford University, California; USNM - National Museum of Natural History, Washington D.C.; WAM - West Australian Museum, Perth; ZMMGU - Moscow State University, Zoological Museum, Moscow; ZMUC - Universitets Zoologisk Museum, Copenhagen.

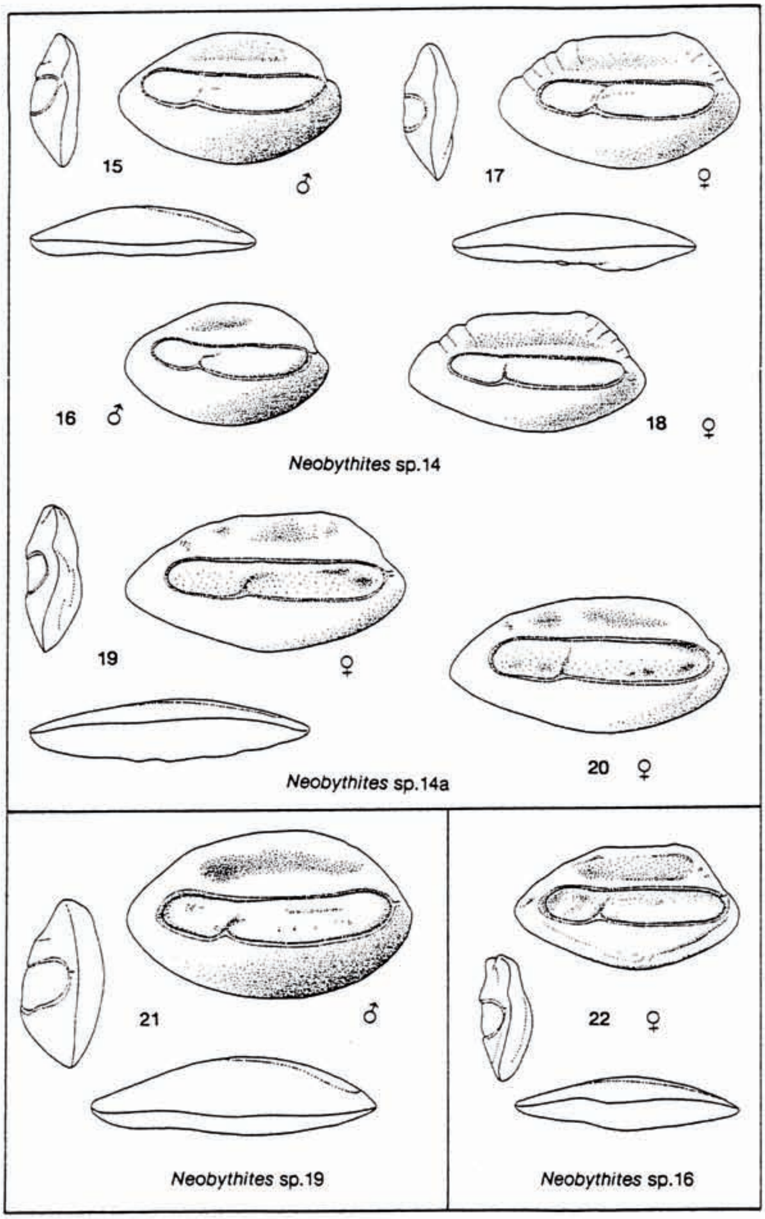


Figs 1-2. - *Neobythites analis* Barnard, 1927; both from off South Africa; fig. 1 = male, off Natal (ZMUC 77817); fig. 2 = female, off Durban (RUSI 12356). 4 X. Fig. 3. - *Neobythites macrops* Günther, 1887; Phillipines, N off Mindanao (10°40'N / 124°15'E), (USNM 099117); male. 4 X. Figs 4-5. - *Neobythites fasciatus* Smith & Radcliffe, 1913; fig. 4 = male, Celebes Sea off Mindanao (08°48'N / 123°27'E), (USNM 099064); fig. 5 = paratype, female, (BMNH 1939.4.1.9.). 4 X.

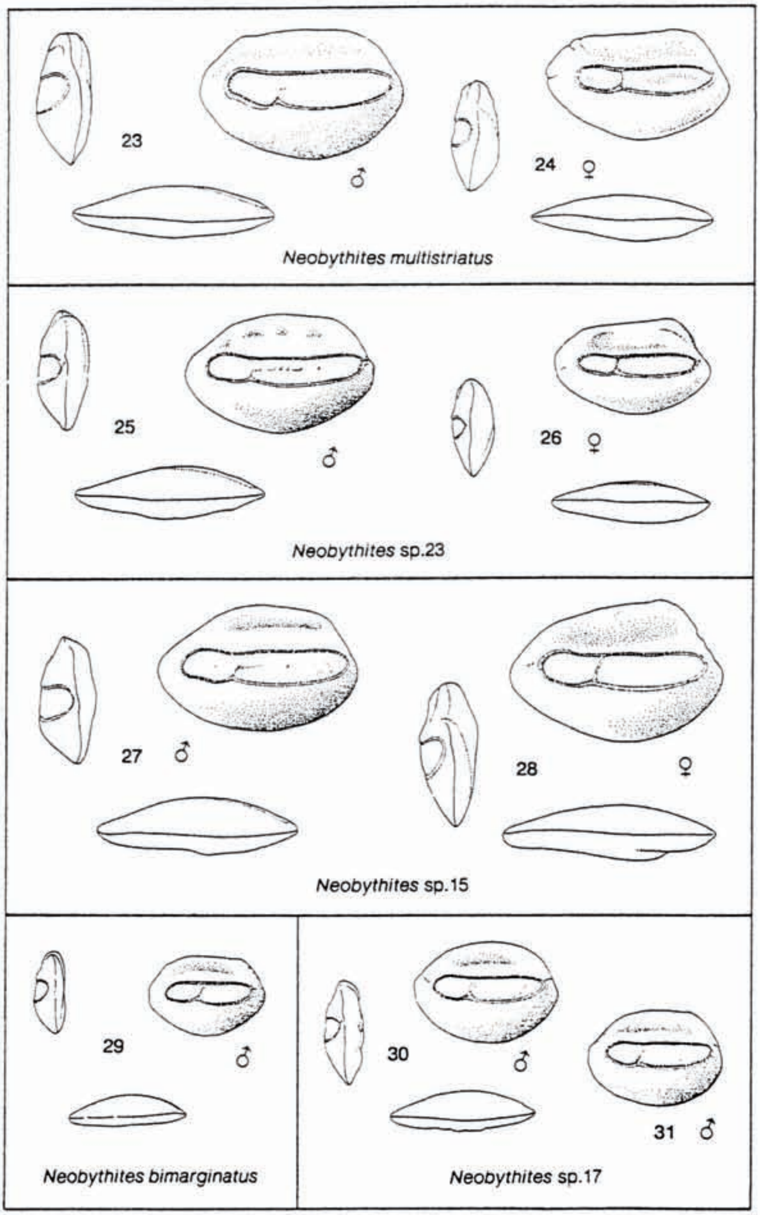




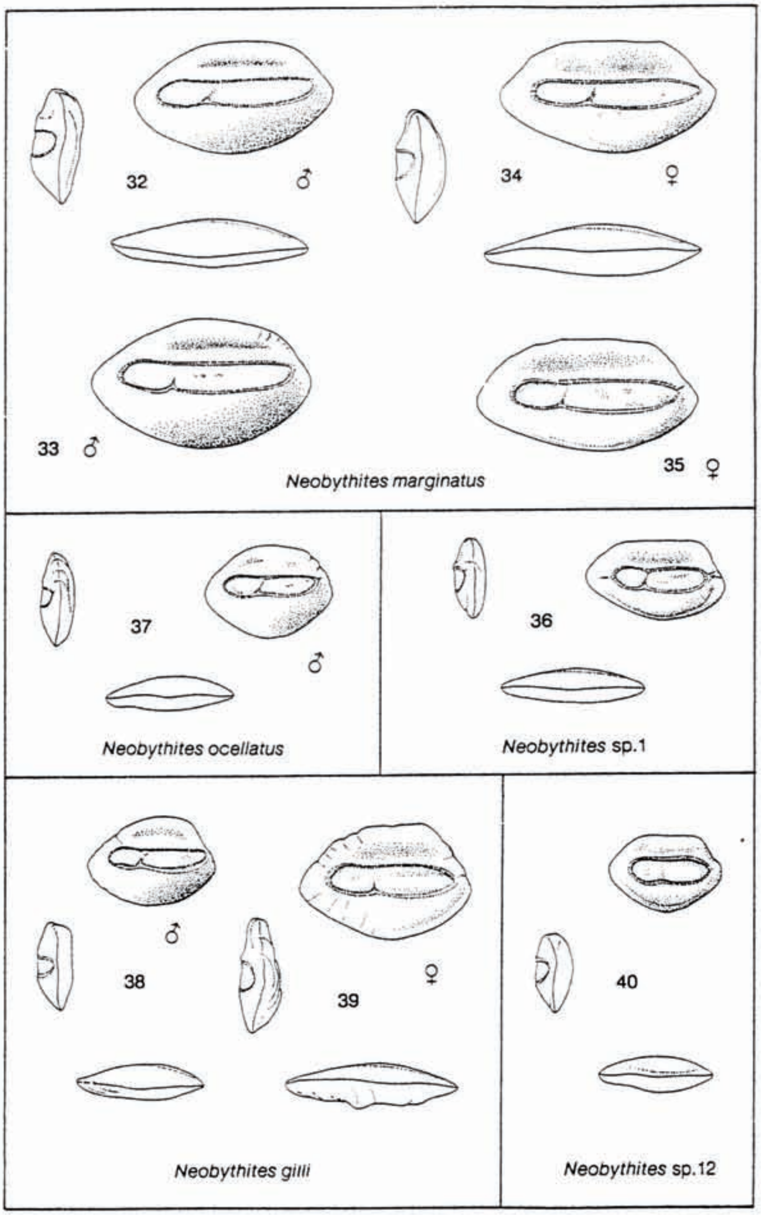
Figs 6-11. - *Neobythites* sp.2; paratypes; figs. 6, 8, 10 = males, fig. 6 (MNHN 1992-530); figs. 8, 10 (ZMUC 77833-34), SW off Madagascar (22°19'S / 43°06'E); figs. 7, 9, 11 = females, (ZMMGU P-18921), SW off Madagascar (22°19'S / 43°06'E). 4 X. Figs 12-14. - *Neobythites* sp.3; fig. 12 = male, paratype (MNHN 1992-533); fig. 13 = male, holotype (ZMMGU P-18904), SW off Madagascar (22°19'S / 43°06'E); fig. 14 = female (eroded by formalin), paratype (MNHN 1992-532), NW off Madagascar (15°24'S / 46°02'E). 5 X.



Figs 15-18. - *Neobythites* sp.14; off Saipan (15°10'N / 143°39'E), (USNM 309006); fig. 15-16 = males (No. 780, 782); fig. 17-18 = females (No. 783, 784). 4 X. Figs 19-20. - *Neobythites* sp.14a; East Karolinas, E of Kapingamarangi, (USNM 309004); females (No. 777, 778). 4 X. Fig. 21. - *Neobythites* sp.19; off Hawai, Caroline Island, (SOSC 23.4.1972); male (No. 819). 4 X. Fig. 22. - *Neobythites* sp.16; South China Sea (16°20'N / 114°39'E), (USNM 309002); female. 4 X.



Figs 23-24. - *Neobythites multistriatus* Nielsen & Quéro, 1991; paratypes, off Réunion; fig. 23 = male, (ZMUC 77809); fig. 24 = female, 20°57'S / 55°14'E, (MNHN 1988-1946). 4 X. Figs 25-26. - *Neobythites* sp.23; off Western Australia (18°05'S / 118°08'E), (LACM 43619-3); fig. 25 = male (No. 790); fig. 26 = female (No. 789). - 5 X. Figs 27-28 .- *Neobythites* sp.15; South China Sea; fig. 27 = male, 16°20'N / 114°39'E, (USNM 309000 - No. 760); fig. 28 = female, 16°11'N / 114°27'E, (USNM 309001 - No. 762). 4 X. Fig. 29. - *Neobythites bimarginatus* Fourmanoir, 1981; paratype, off New Caledonia, (MNHN 1978-No. 473); male. 4 X. Figs. 30-31 - *Neobythites* sp.17; (AMS I.25826-008); male. 4 X.



Figs 32-35. - *Neobythites marginatus* Goode & Bean, 1886; figs. 32, 33 = males; fig. 32 off Bahamas (24°52'N / 83°37'W), (ZMUC 77568); fig. 33 off Dry Tortugas (24°31'N / 83°24'W), (USNM 308898 - No. 738); figs. 34, 35 = females; fig. 34 off Dry Tortugas (24°31'N / 83°34'W), (USNM 308898 - No. 739); fig. 35 off Blake Plateau, (MCZCM 28154). 4 X. Fig. 36. - *Neobythites* sp.1; sex not identified, off Brazil near Amazon river mouth, (USNM 308991) (01°51'N / 46°50'W). 4 X. Fig. 37. - *Neobythites ocellatus* Günther, 1887; holotype, male, off Brazil (BMNH 1887.12.7.43). 4 X. Figs 38-39. - *Neobythites gilli* Goode & Bean, 1886; fig. 38 = holotype, male, Gulf of Mexico W off Florida (28°36'N / 85°33'W), (USNM 037340); fig. 39 = female, Atlantic off Panama (09°04'N / 81°25'W), (USNM 308899). 4 X. Fig. 40 - *Neobythites* sp.12; SE off Lombock Island, Indonesia, (ZMUC 77744); assumed male. 4 X.

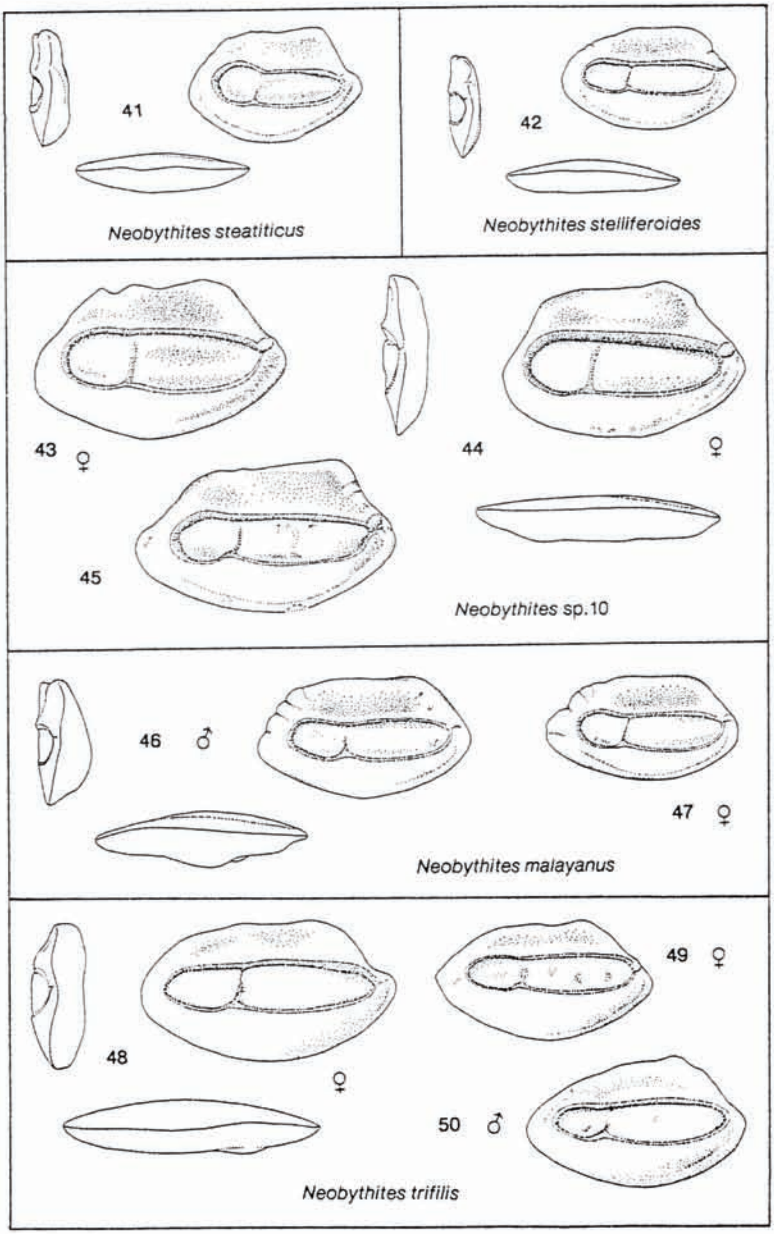


Fig. 41. - *Neobythites steatiticus* Alcock, 1893; Bay of Bengal, (USNM 287242). 4 X. Fig. 42. - *Neobythites stelliferoides* Gilbert, 1890; Gulf of Panama (07°N / 79°W), (ZMUC 77684). 4 X. Figs 43-45. - *Neobythites* sp.10; Gulf of Aden; fig. 43 = female, (ZMUC 77841), (13°09'N / 45°41'E); fig. 44 = female, (ZMMGU P-18928), (13°13'N / 45°41'E); fig. 45 ("sp.9") USNM 302930, (11°10'N / 48°11'E). 4 X. Figs 46-47. - *Neobythites malayanus* Weber, 1913; fig. 46 = male, off Sumbawa, Indonesia, (ZMUC unreg.); fig. 47 = female, Celebes Sea off Phillipines (06°50'N / 126°14'E), (USNM 099054). 4 X. Figs 48-50. - *Neobythites trifilis* Kotthaus, 1979; off Chagos Islands (10°19'N / 59°08'E), (USNM 308998); figs. 48, 49 = females; fig. 50 = male ?. 4 X.

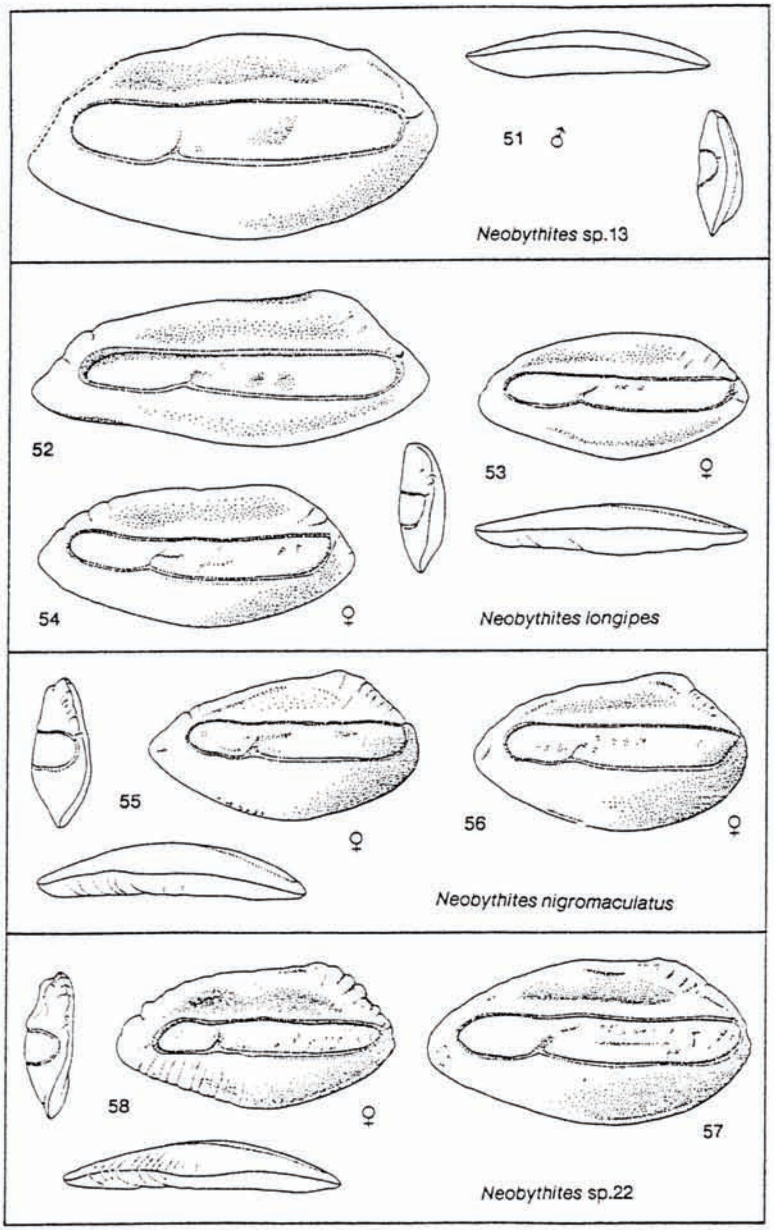
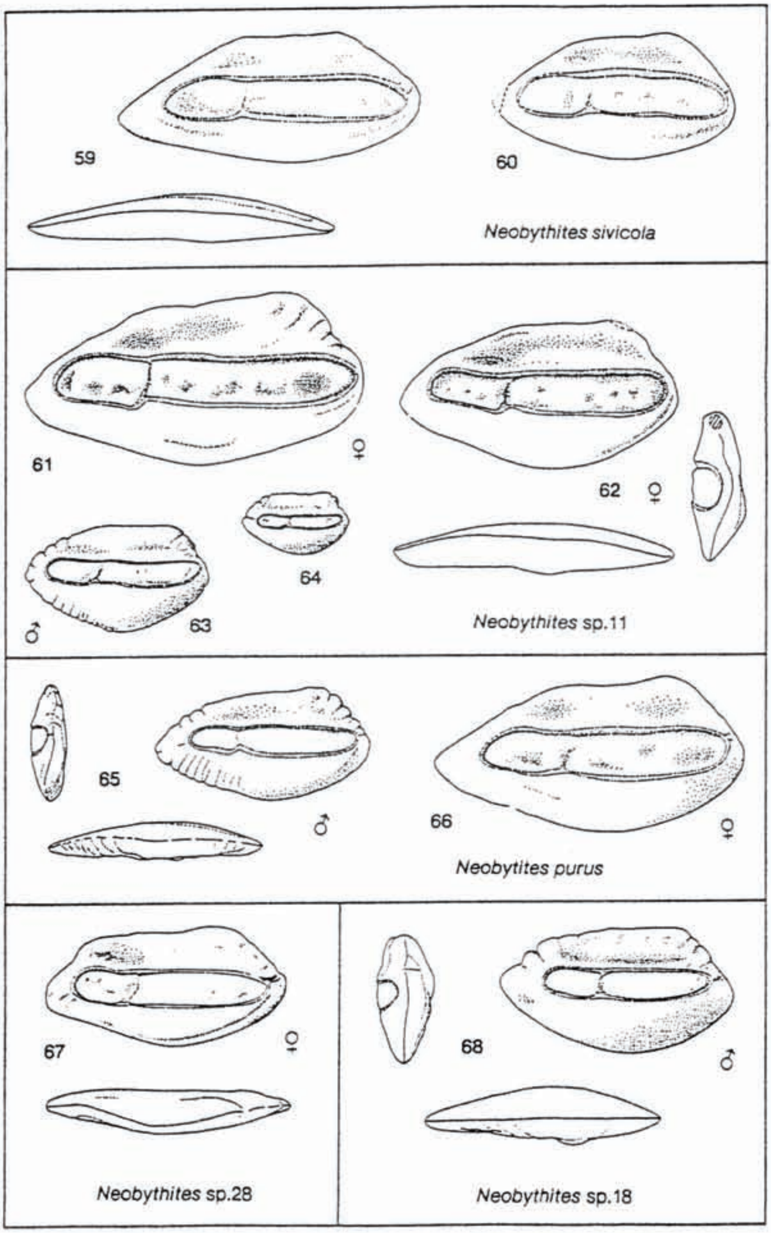


Fig. 51. - *Neobythites* sp.13; male ?, (Hobart CA 3814 - No. 638). 4 X (lateral views 2.65 X). Figs 52-54. - *Neobythites longipes* Smith & Radcliffe, 1913; fig. 52 off Phillipines (05°50'N / 120°31'E), (USNM 99070; otolith coll. IRSNB); figs. 53, 54 = females, Celebes Sea off Borneo (06°01'N / 120°44'E), (USNM 99091). 4 X. Figs 55-56. - *Neobythites nigromaculatus* Kamohara, 1938; Japan, Kochi, Mimose fish market, (two specimens from BSKU 3574, 37006, 37542, 39948, 39998, 44500), females. 4 X. Figs 57-58. - *Neobythites* sp.22; off Western Australia; fig. 57 (WAM; otolith coll. ISH, leg Schwarzhans - specimen figured by Schwarzhans,1981 as *N. gilli*); fig. 58 (18°04`S / 118°222'E), (LACM 43621-1 - No. 788), female. 4 X.



Figs 59-60. - *Neobythites sivicola* (Jordan & Snyder, 1901); fig. 59 Japan, Misaki, (SU 23473; otolith coll. IRSNB); fig. 60 Japan, Kochi, Mimose fish market, (ZMUC unreg.). 4 X. Figs 61-64. - *Neobythites* sp.11; figs. 61 (CSIRO 2310.01-05), female; fig. 62 (Hobart 594-03/04 - No. 646), female; figs. 63, 64 (CSIRO) (fig. 63 = male). 4 X. Figs 65-66. - *Neobythites purus* Smith & Radcliffe, 1913; fig. 65 RW Coriolis St. 10 off Manila Bay, (MNHN, Coll. Fourmanoir), male ?; fig. 66 Arafura Sea off Tanimbar (09°09'S / 131°48'E), (ZMUC 77757), female. 4 X. Fig. 67. - *Neobythites* sp.28; off Bali, (ZMUC - No.861), female. 2.65 X. Fig. 68. - *Neobythites* sp.18; Lombock Strait off Bali, (ZMUC 77743), male. 4 X.

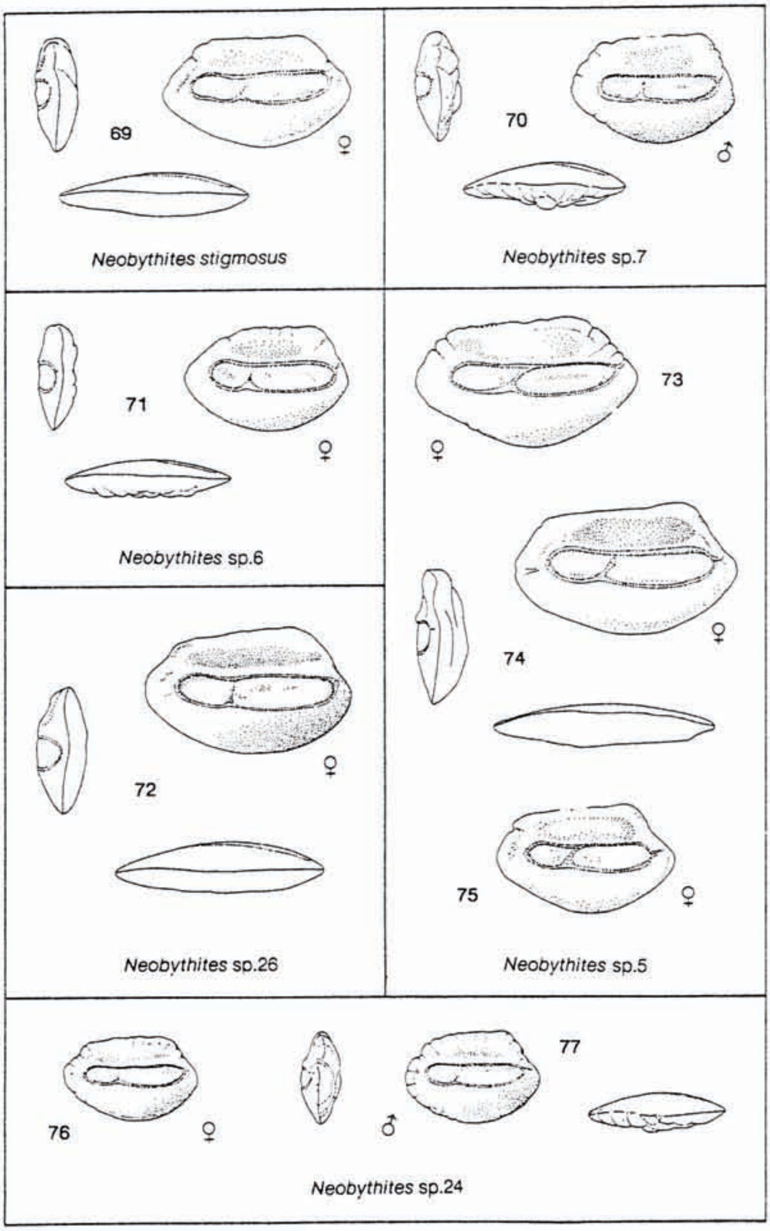


Fig. 69. - *Neobythites stigmosus* Machida, 1984; Japan, Tosa Bay, (JM P 77811-14), female. 4 X. Fig. 70. - *Neobythites* sp.7; holotype (RUSI 13952), male. 4 X. Fig. 71. - *Neobythites* sp.6; Seychelles-Mauritius ridge (11°02'S / 62°15'E), (IOAN), female. 4 X. Fig. 72. - *Neobythites* sp.26; off Fiji Islands, (BMNH 1887.12.7.42), (syntype of *N. macrops*), female. 4 X. Figs 73-75. - *Neobythites* sp.5; females; fig. 73 off Somalia (11°35'N / 52°54'E), (ZMMGU P-18907); figs. 74, 75 off Amirantes, (ZMMGU P-18911 and ZMUC 77839). 4 X. Figs 76-77. - *Neobythites* sp.24; off New South Wales, (LACM 42620-2); fig. 76 female (No. 793); fig. 77 male (No. 794). 4 X.

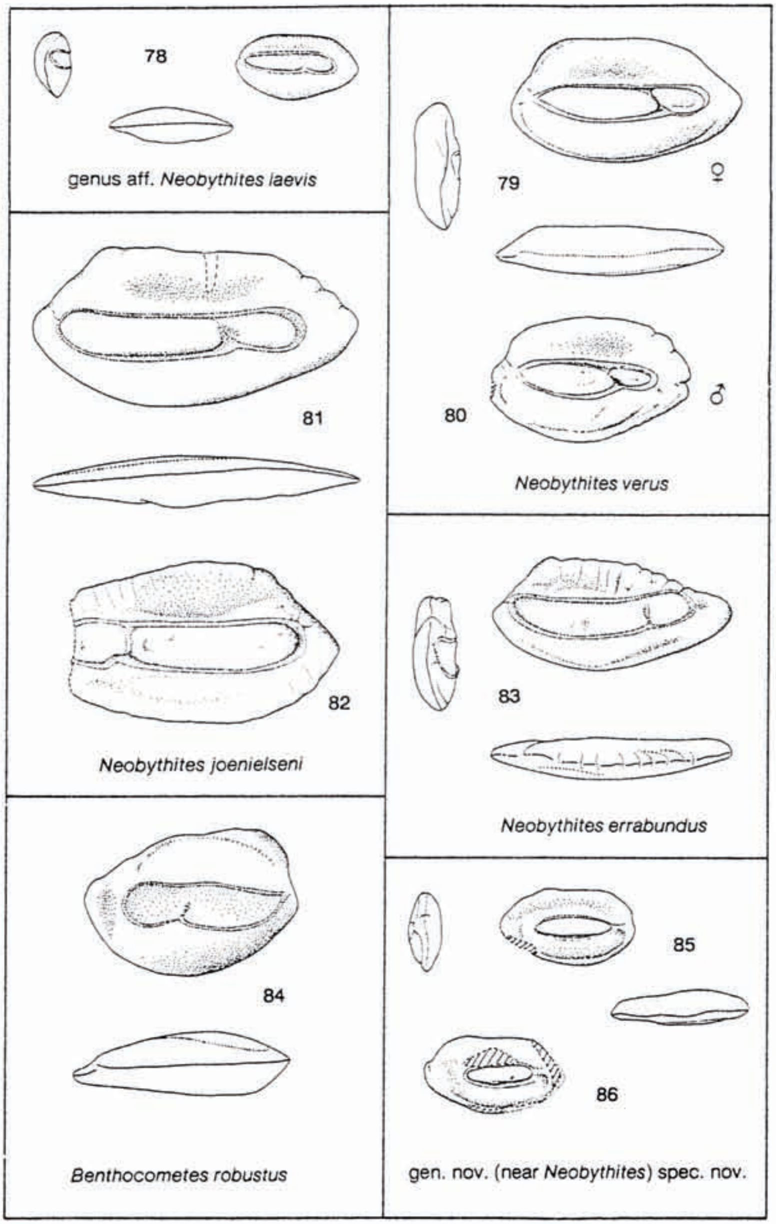
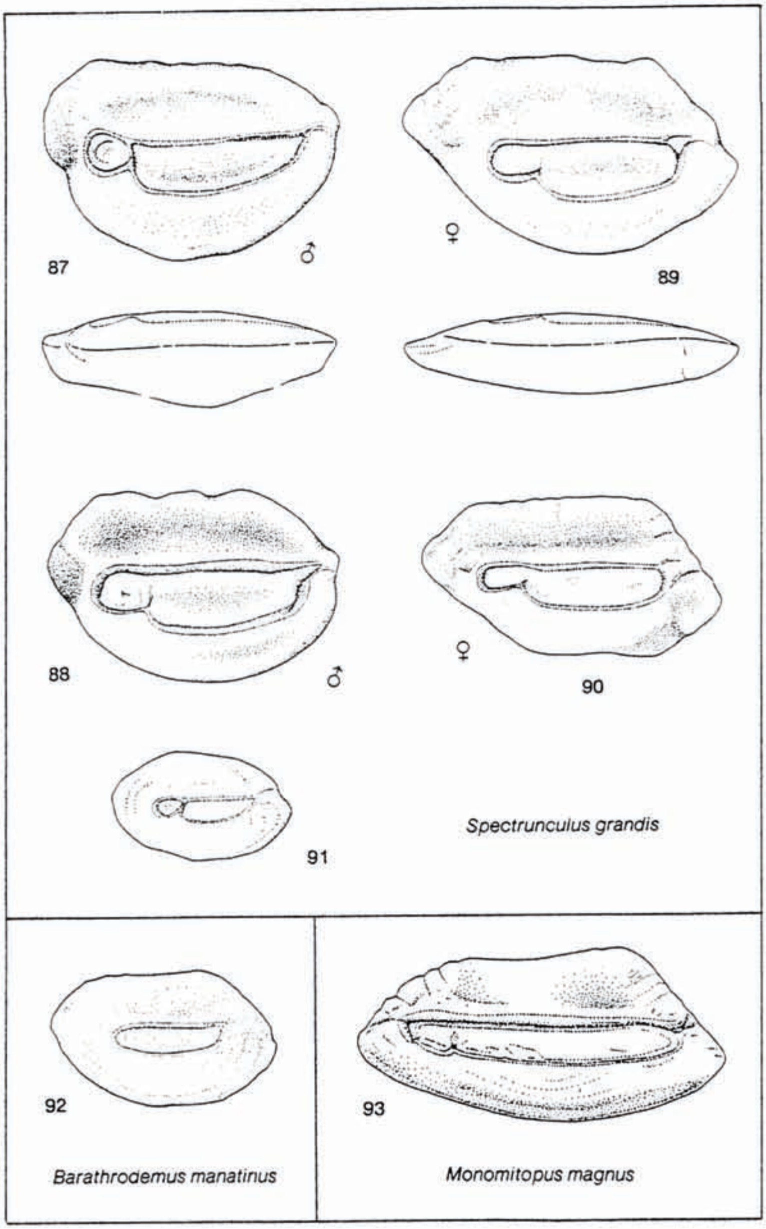
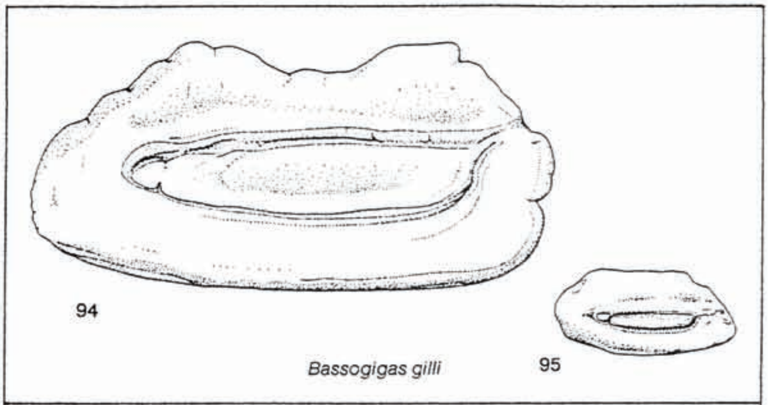

78
genus aff. *Neobythites laevis*
79
♀
80
♂
Neobythites verus
81
82
Neobythites joenielseni
83
Neobythites errabundus
84
Benthocometes robustus
85
86
gen. nov. (near *Neobythites*) spec. nov.

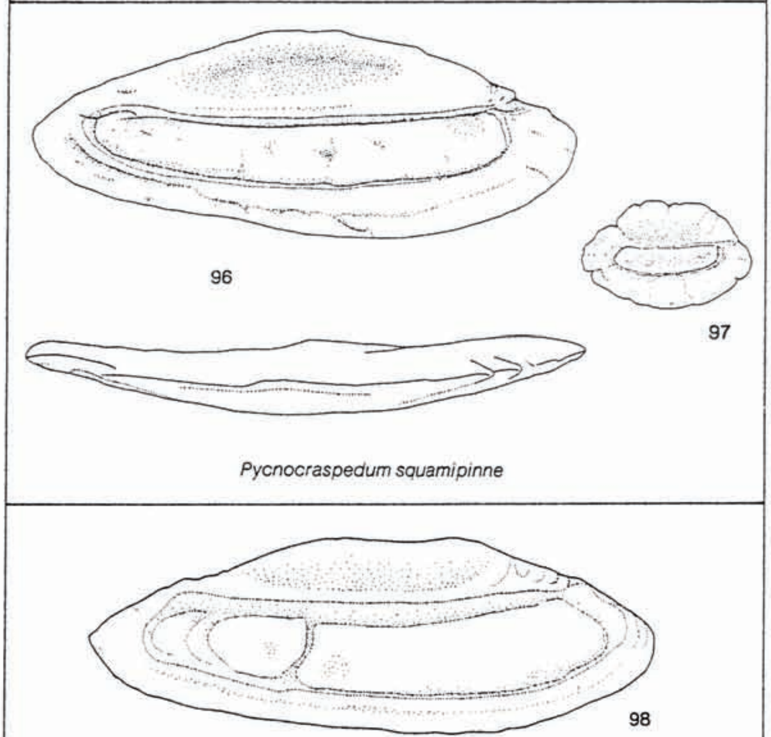
Fig. 78. - Genus aff. *Neobythites laevis* Stinton, 1977; holotype, Selsey Fm., Middle Eocene, Selsey, Sussex, New Hampshire Basin, England, (BMNH P. 57818). 7.75 X. Figs. 79-80. - *Neobythites verus* Schwarzhans, 1986; fig. 79, holotype of *N. verus* (assumed female), (SADME 10302), Aldingian (P 15), Upper Eocene, New Morphett St. Bridge Bore 5 (100-108'), Adelaide, St. Vincent Basin, South Australia; fig. 80, holotype of *N. inprobus* (assumed male), (SADME 10303), Aldingian (P 16), E & W Coonalpyn Bore 2 (330-335'), Murray Basin, South Australia. 8 X. Figs 81-82. - *Neobythites joenielseni* n.sp.; fig. 81, holotype, (BSP), Altonian, Lower Miocene, Pukeuri road cut, Otago, New Zealand South Island; fig. 82, paratype, (GSNZ), Waiauan, Middle Miocene, Karoro brick work, Westland, New Zealand South Island. fig. 81 = 4 X; fig. 82 = 2.85 X. Fig. 83. - *Neobythites errabundus* n.sp.; holotype, (GPIM-M), Reinbek, Middle Miocene, Laerhof water well, Kevelaer-Wetten, Northwest Germany, North Sea Basin. 2.65 X. Fig. 84. - *Benthocometes robustus* (Goode & Bean, 1886); off Sardinia, Mediterranean, (otolith IRSNB). 4 X. Figs 85-86. - gen. nov. (near *Neobythites*) spec. nov.; off Japan; fig. 85 = (BSKU 19513); fig. 86 = (BSKU 19514). 4 X.



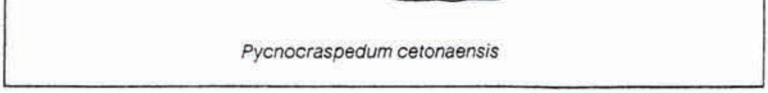
Figs 87-91. - *Spectrunculus grandis* (Günther, 1877); figs. 87, 88 = males, (BMNH, CH 89/92/1 - coll. N. Merrett); figs. 89, 90 = females, (BMNH, CH 89/92/1 - coll. N. Merrett); fig. 91 = juvenile, off South Africa, (otolith ISH; leg. ZMUC). 4 X. Fig. 92. - *Barathrodemus manatinus* Goode & Bean, 1883; off Florida, (otolith LACM; coll. Fitch). 12.2 X. Fig. 93. - *Monomitopus magnus* Carter & Cohen, 1985; paratype, 29°46'N / 27°09'W, (ZMUC 77754). 2.5 X.



Bassogigas gilli

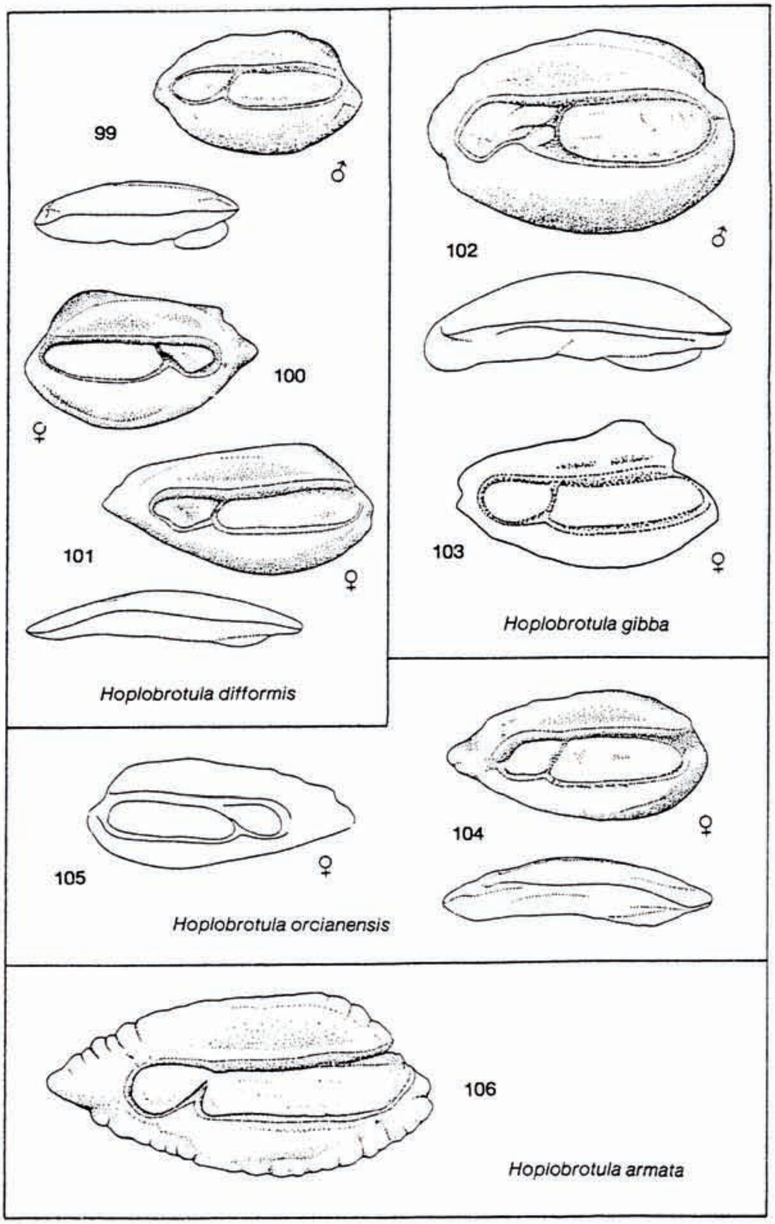


Pycnocraspedum squamipinne



Pycnocraspedum cetonaensis

Figs 94-95. - *Bassogigas gilli* Goode & Bean, 1896; fig. 94, adult, off Cape Town, South Africa, (ZMUC unreg.); fig. 95, juvenile, 36°39'N / 74°11'W, (USNM 215299). 4 X. Figs 96-97. - *Pycnocraspedum squamipinne* Alcock, 1889; fig. 96, adult, off Madagascar (22°21'S / 43°04'E), (ZMUC unreg.); fig. 97, juvenile, off Zanzibar Island, (otolith IRSNB). 4 X. Fig. 98. - *Pycnocraspedum cetonaensis* (Schwarzhans, 1978); holotype, (SMF P.5694), Zanclian, Lower Pliocene, Cetona near Siena, Toscana, Italy, Mediterranean Basin. 4 X.



Figs 99-101. - *Hoplobrotula difformis* (Koken, 1884); fig. 99, assumed male, (coll. Schwarzhans), Reinbek, Middle Miocene, Dingden, Northwest Germany, North Sea Basin; fig. 100, assumed male (lectotype of *H. joachimica*), (SMF P.1113a), Rupel, Middle Oligocene, Joachimsthal, Chekoslovakia, Vienna Basin; fig. 101, assumed female (holotype of *H; elongata*), (SMF P.3190), Middle Miocene, well near Venlo, Netherlands, North Sea Basin. 4 X. Figs 102-103. - *Hoplobrotula gibba* (Bassoli, 1906); Tortonian, Upper Miocene, St. Agatha di Tortona, Toscana, Mediterranean Basin; fig. 102, assumed male, (Roemer Mus. Hildesheim); fig. 103, assumed female (schematic redrawing of Robba's holotype). fig. 102 = 4 X; fig. 103 = 2.5 X. Figs 104-105. - *Hoplobrotula orcianensis* n.sp.; Zanclian, Lower Pliocene, Orciano near Pisa, Tosacana, Italy, Mediterranean Basin; fig. 104 holotype, (BMNH P.41581); fig. 105 paratype (eroded specimen), (BMNH P.41538). 4 X. Fig. 106. - *Hoplobrotula armata* (Temminck & Schlegel, 1846); off New South Wales (29°43'S / 153°55'E), (AMS 21799-001). 4 X.